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HOW DO THE MODIFIERS OF LINKAGE VALUES AFFECT
DETACHED PORTIONS OF THE CHROMOSOME?

BY

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THESIS

FOR THE

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IS APPROVED BY ME AS FULFILLING THIS PART OF THE REQUIREMENTS FOR THE

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HOW DO THE MODIFIERS OF LINKAGE VALUES AFFECT DETACHED PORTIONS OF THE CHROMOSOME?

I

INTRODUCTION

The amount of literature that has been published recently bearing on the phenomenon of linkage of hereditary factors makes it unnecessary to give any description of the same at this time. To explain the vast accumulation of data obtained from intelligently planned, and carefully controlled experiments, several theories have been advanced; but as time goes on it is becoming more and more obvious that the chiasmatype theory is the most plausible. According to the chiasmatype theory, Mendelian factors, or genes, reside in a linear series on the chromosomes, and each has a definite locus with its allelomorph occupying the corresponding locus on the other member of the homologous pair of chromosomes. The immediate cause of crossing over is attributed to the breaking of the homologous pair of chromosomes, which twist around each other during synapsis, and the subsequent reunion of them, each taking a piece that formerly belonged to the other.

Taking this theory as a working basis, geneticists had accumulated sufficient data to convince themselves, until quite recently, that the crossover value between two Mendelian factors, is constant and invariable. It is the amount of such data and the accepted concept of the linear arrangement of genes on the chromosome that led Morgan to believe that crossover value between two linked factors is a function of distance. Attractive and suggestive as Morgan's postulate may be, it has not been wholly successful, however, in placing itself beyond question. New searches were conducted by different investigators and

they have shown that crossover values are variable, being influenced by age (Bridges '16), temperature (Plough '17), and also certain specific genetic factors (Sturtevant '17).

The array of evidence against Morgan's view was amplified by the work of Detlefsen and Roberts (Detlefsen and Roberts '21) who worked on *Drosophila*, and through selection have been able to reduce a crossover value of 33% (from white to miniature), to practically zero, in one of the series at the end of the 12th generation. Instead of accepting Morgan's hypothesis of distance, Detlefsen ('21) propounds that the linkage value is at least to a large extent "determined by the different possible combinations of multiple modifying factors." In order to test out this view, he actually performed a hybridization experiment between the low crossover stock and normal flies. A portion of his data is reproduced in Table I. In the table, there are to be found in the first and second lines the distributions of crossover values of normal populations and F_1 generation of series B. In F_{42} generation of series B low stock, he mated fifty red long females to normal white miniature males, and the crossover values of these females are shown in the third line. To secure a representative distribution of crossover values of the F_1 hybrid females thus derived, he chose four such females from each of the forty-four P_1 pairs and crossed them to their brothers. The distribution of such a population is given in the fourth line. It is stated that since it is impossible to test out the crossover capacity of the male parents, we must accept for them the value of series B F_1 generation, since they came from a stock which had been used for class work for many years and always found to give a value approximating 33%. The F_2 distribution shown here is the total of three distinct and separate F_2 distributions which came from P_1 pairs No. 2, 5 and 6. It is almost needless to point out that the F_1 distribution lies in between those of the two parents and so do both the value of the mean variate and mean total

TABLE I

The distribution of Crossover Values in Normal Population, in Low Crossover Stock and in Hybrids

Between These - After J. A. Detlefsen.

Generation	No. of vari-ates	The distribution of crossover values															Mean vari-ates	σ	Total crossovers	% of Total crossovers	Average no. of progeny overs per vari-ate
		15	45	75	105	135	165	195	225	255	285	315	345	375	405						
Sample Population	88								7	11	19	28	15	5	3	3055	4.28	1465	21071	70.68	239.4
1st Generation Series B	34							3	5	3	10	6	3	2	2	2885	5.58	2056	7189	28.60	211.4
P1 Low Parent	49	7	26	15	1											511	2.10	425	7948	5.35	162.2
F1 Sample of each P1	45			10	18	10	6	1								1150	3.10	5213	39416	13.23	875.9
F2 Total	148	2	2	8	27	44	39	14	5	5	1					1466	4.81	5698	38514	14.79	260.2

crossover value. The F_2 has a wider range of distribution than that of the F_1 ; but the values of the mean variates and the mean total crossover values is about the same as the F_1 . Such features characterizing a hybridization experiment where multiple factors with incomplete dominance are involved are further confirmed by the increased standard deviation of the F_2 distribution. It is this and other genetic analyses that led Detlefsen ('21) to wonder "just what part distance between two genes on a chromosome map may play in determining linkage values."

The present work, which is really a minor part of his, was undertaken with the hope of throwing further light on the whole problem by attempting to find out how the modifiers of linkage values affect detached portions of the chromosome. Would the separated pieces still give low values, or would they behave in some other fashion?

II

MATERIALS AND METHODS.

To cope with the complexity of such an experiment, Professor Detlefsen developed a special system of designation which I shall use in the following description. According to this system, the piece of chromosome between white and miniature is divided into three different regions as shown in Figure 1. Individuals carrying the different pieces of chromosomes are named accordingly. For instance, individuals carrying the piece of chromosome from red to cross-veined and the rest of the chromosome comes from the other member of the homologous pair is considered as Region 1. Those carrying the pieces from cross-veined to not-cut is called Region 2, etc. The shaded portion in the figure represents the region outside of selection. With reference to this region a more detailed discussion will appear in the latter part of this paper.

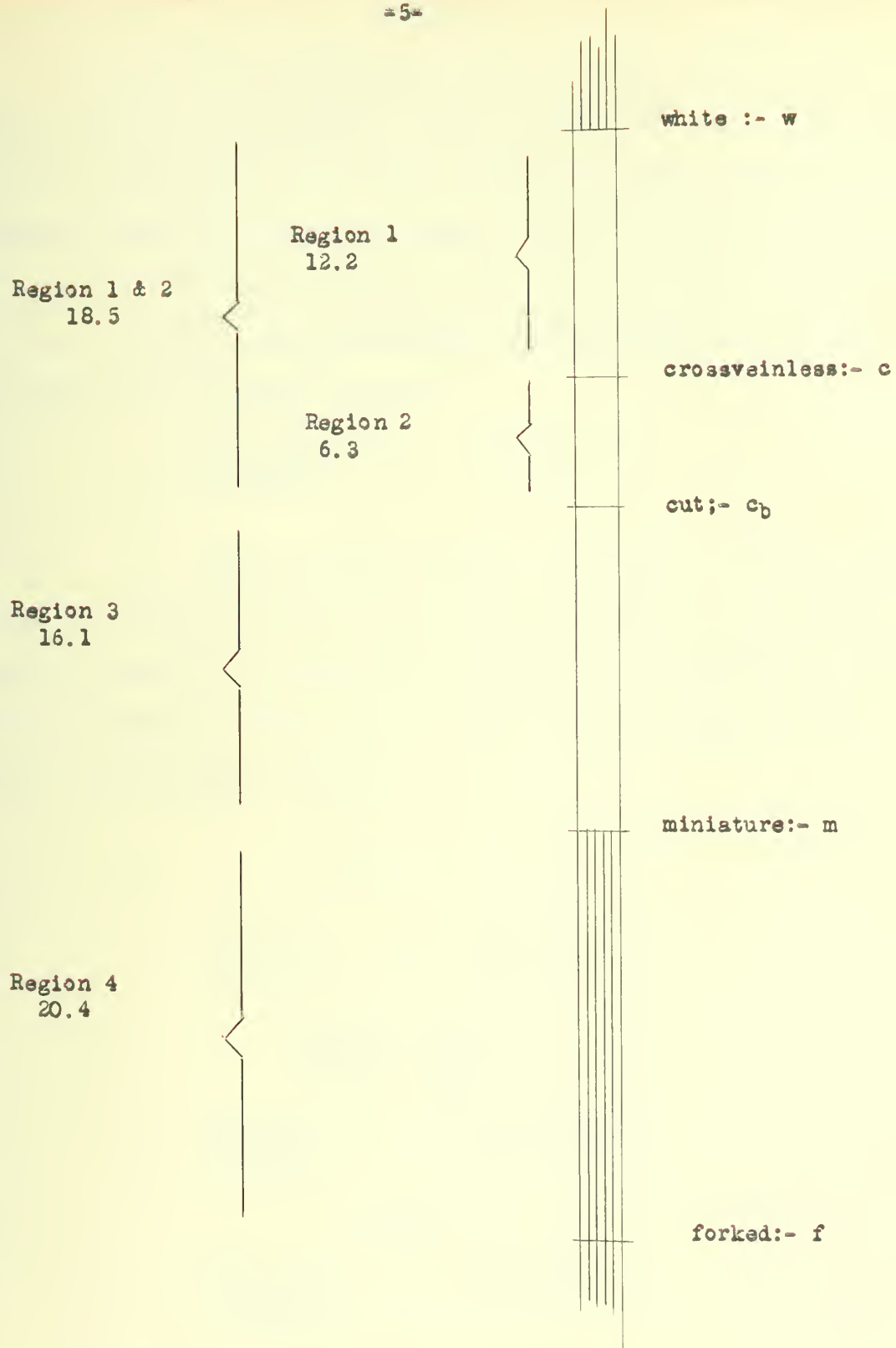


Fig. I. Showing the relative positions of the different factors involved in the experiment, and the meaning of "Region". The shaded portion represents the region that is outside of selection influence.

The origin of our experimental materials was as follows: Mr. L. S. Clemente crossed normal homozygous recessive females of the zygotic constitution, w,c,c_b,m,f:- white (eye) cross veinless (wing), cut (wing), and forked (bristle) to a dominant male of the genetic formula, W,C,C_b,M,F (red, cross-veined, not cut, long, and not forked) which he obtained from Prof. Detlefsen's low crossover stock F₇₈. As usual he secured homozygous recessive males and dominant females heterozygous for the factors involved:-

$$\begin{array}{c} w \ c \ c_b \ m \ f \\ \hline W \ C \ C_b \ m \ f \end{array} \quad \begin{array}{c} \text{♀} \\ + \\ \text{♂} \end{array} \quad \begin{array}{c} w \ c \ c_b \ m \ f \\ \hline w \ c \ c_b \ m \ f \end{array}$$

Mating the sibs together, crossovers in various regions were obtained. Mr. Feldman took over the females of Region 1 & 2, and Region 4 was run by myself. Among these various region crossovers, we secured those of Region 1 & 2 and those of Region 4. The process in which they are supposed to have evolved is shown in the following diagram:-

Region 1 & 2

$$\begin{array}{c} W \ C \ C_b \ M \ F \\ \hline w \ c \ c_b \ m \ f \end{array} \quad \times \quad \begin{array}{c} w \ c \ c_b \ m \ f \\ \hline w \ c \ c_b \ m \ f \end{array}$$

$$\begin{array}{c} W \ C \ C_b \quad m \ f \\ \hline w \ c \ c_b \quad M \ F \end{array}$$

$$\begin{array}{c} W \ C \ C_b \ m \ f \quad \text{♀} \\ \hline w \ c \ c_b \ m \ f \end{array} \quad \begin{array}{c} W \ C \ C_b \ m \ f \quad \text{♂} \\ \hline W \ C \ C_b \ m \ f \end{array}$$

Region 4

$$\begin{array}{c} W \ C \ C_b \ M \ F \\ \hline w \ c \ c_b \ m \ f \end{array} \quad \times \quad \begin{array}{c} w \ c \ c_b \ m \ f \\ \hline w \ c \ c_b \ m \ f \end{array}$$

$$\begin{array}{c} W \ C \ C_b \quad m \ f \\ \hline w \ c \ c_b \quad M \ F \end{array}$$

$$\begin{array}{c} w \ c \ c_b \ M \ F \\ \hline w \ c \ c_b \ m \ f \end{array} \quad \begin{array}{c} w \ c \ c_b \ M \ F \\ \hline w \ c \ c_b \ M \ F \end{array}$$

A list of the classes of offspring obtained from Region 1 & 2
and Region 4 females.

		<u>Region 1 & 2</u>				
		W	C	C _b ^{♀♀}	W	C C _b ♂♂
Parental ---		<u>W</u>	<u>C</u>	<u>C_b</u>	<u>W</u>	<u>C C_b</u>
		w	c	c _b	w	c c _b
		<u>W</u>	<u>C</u>	<u>C_b</u>	<u>W</u>	<u>C C_b</u>
Crossover ---		w	c	c _b	w	c c _b
		<u>W</u>	<u>C</u>	<u>C_b</u>	<u>W</u>	<u>C C_b</u>
		w	c	c _b	w	c c _b
Crossover ---		<u>W</u>	<u>C</u>	<u>C_b</u>	<u>W</u>	<u>C C_b</u>
		w	c	c _b	w	c c _b
		<u>W</u>	<u>C</u>	<u>C_b</u>	<u>W</u>	<u>C C_b</u>
Crossover ---		w	c	c _b	w	c c _b
		<u>W</u>	<u>C</u>	<u>C_b</u>	<u>W</u>	<u>C C_b</u>
		w	c	c _b	w	c c _b
Crossover ---		<u>W</u>	<u>C</u>	<u>C_b</u>	<u>W</u>	<u>C C_b</u>
		w	c	c _b	w	c c _b
		<u>W</u>	<u>C</u>	<u>C_b</u>	<u>W</u>	<u>C C_b</u>
Crossover ---		w	c	c _b	w	c c _b
		<u>W</u>	<u>C</u>	<u>C_b</u>	<u>W</u>	<u>C C_b</u>
		w	c	c _b	w	c c _b
		<u>Region 4</u>				
Parental ---		<u>M</u>	<u>F</u>	<u>F</u>	<u>M</u>	<u>F</u>
		m	f	f	m	f
		<u>M</u>	<u>F</u>	<u>F</u>	<u>M</u>	<u>F</u>
Crossover ---		m	f	f	m	f
		<u>M</u>	<u>F</u>	<u>F</u>	<u>M</u>	<u>F</u>
		m	f	f	m	f
Crossover ---		<u>M</u>	<u>F</u>	<u>F</u>	<u>M</u>	<u>F</u>
		m	f	f	m	f
		<u>M</u>	<u>F</u>	<u>F</u>	<u>M</u>	<u>F</u>

These crossovers made up the material of Experiment 1.

Experiment 2 had a somewhat similar origin. In Experiment 2, the male that originated the population was from F_{84} generation of Dr. Detlefsen's low crossover stock and the females to which it was mated came from a quadruple recessive stock which had been subjected to six generations of inbreeding. This quadruple recessive stock was a white, cut, cross veinless, miniature.

Our methods of procedure with the F_2 segregates of the various regions are the same, for females carrying any given region were mated to the ultimate recessive males. The different classes of offspring resulting from these two crosses are shown in the accompanying chart. Each female was kept with three or four males of the right kind in 8-drachm homeopathic vials. The common method of culture for *Drosophila* was followed. Flies were removed to new vials every other day and a new supply of males was introduced to take the place of the dead ones, should deaths occur. Nine days, from the day when the first offspring emerged, were allowed for the last one to be hatched out in each vial, and three countings were made during the nine days. All calculations were done twice on one of the best calculating machines on the market, and it is hoped that arithmetical errors have been reduced to a minimum.

III

DATA AND DISCUSSION.

A - Region 1 and 2.

The distributions of cross over values for Region 1 and 2 in each experiment separately and combined into a total are given. They are plotted in class intervals of 1.5%. The distribution for Experiment 1 ranges from 0 to 18.5% and for Experiment 2 from 0 to 14.25%. The total of the two combined is shown in the last line in the table, and the curves plotted from them are shown in

TABLE 2

Region 1 & 2

Generation	Condition of chromosome	No. of females	Distribution of crossover value												Mean vari-ate
			75	225	375	525	675	825	975	1125	1275	1425	1575	1725	
P ₁	whole		x												
F ₁ Exp. I	"		3	3	2	4	4	3	3	1	1				
F ₂ Exp. I	detached	45	13	5	8	4	2	3	1	1	3	3	1	0	4.51±.321
F ₁ Exp. II	whole														
F ₂ Exp. II	"														
F ₂ Exp. II	detached	58	14	5	8	13	5	5	2	1	2	3			4.98
F ₁ Exp. I&II	whole														
F ₂ Exp. I&II	detached	103	27	10	16	17	7	8	3	2	5	6	1	0	4.12±.194

Total Crossovers	Crossover value	Offspring per female	Reg. 1 crossover %		Reg. 2 crossover %		The crossover value for the generation to which the two low males belong.

5867	320	101	3.18	2.26		8.09
30673	2021					
18427	1072	80	3.55	2.72		3.04
3634	232					
9501	552	90.5	3.41	2.49		



Figure 2.

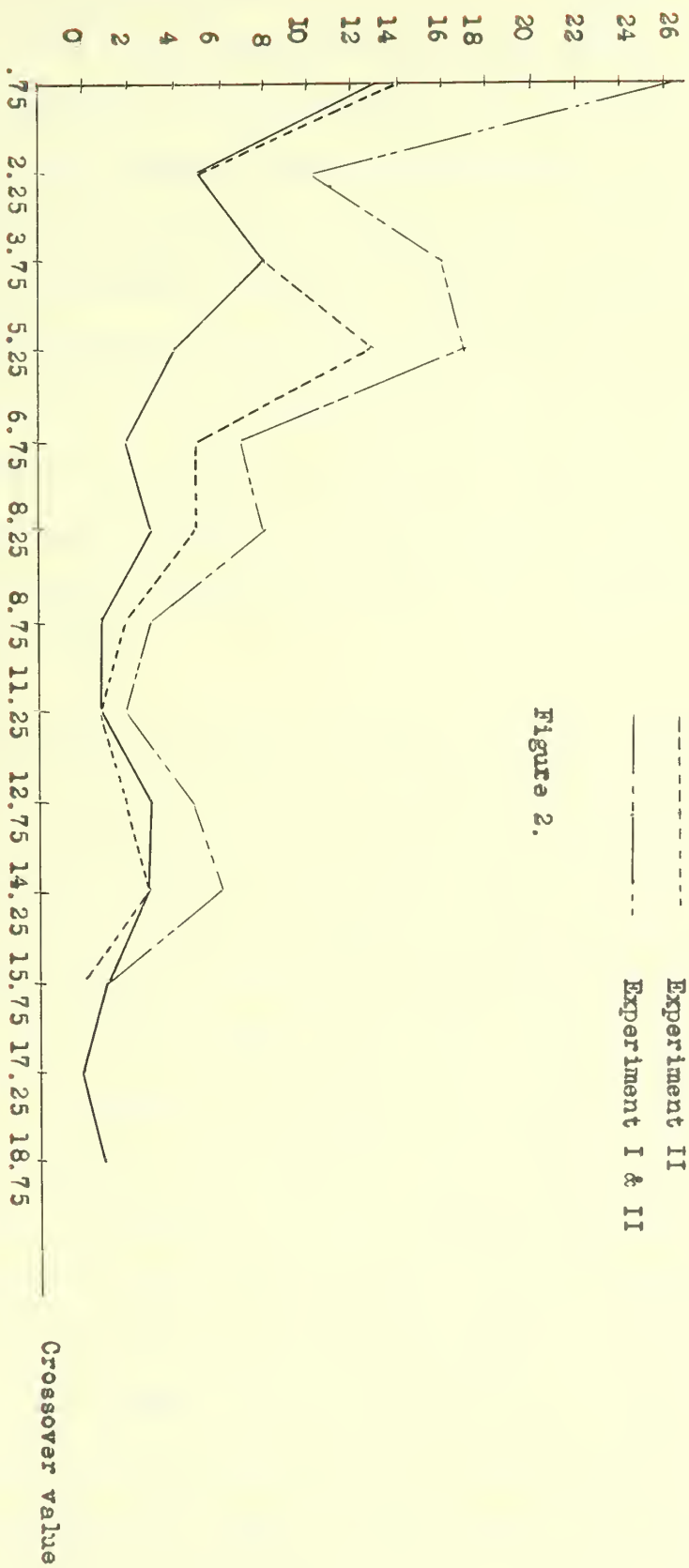


Figure 2. The most striking feature of the curves is the large number of individuals in the first class, making them look rather unique for the experiment. However, if we turn to the back and look through Tables 5 and 6, we will find that there are quite a few of the F_2 segregates giving such a small number of offspring that their crossover values reached zero. It is true that zero percent crossover value should be expected to occur in this case, if we expect modifiers of linkage values to segregate at all; but still we should not overlook the fact that over half of the individuals that give zero percent are those that have exceptionally small number of offspring. Therefore due allowance must be made on the first class in Table 2, and thus the modal classes of the curves could be shifted to 5.25% for Experiment 2 and 3.75% for Experiment 1 and Experiment 1 and 2 combined.

From the description given in the early part of this paper, it is very obvious that we have also performed a hybridization experiment on two strains of *Drosophila* differing from each other in their capacity for crossing over. In fact, as has been shown, this has been admirably done by Prof. Detlefsen himself. The only point in which his work differs from mine lies in the fact that he used the whole region between white and miniature; while I dealt with segments of it. Due to lack of experience in handling the material, and in the method of culture, the results obtained could be much better. There are, however, reflected in the data a few features that are characteristic of a hybridizing^{ation} experiment where multiple factor inheritance with incomplete dominance is involved. These features stand out so strikingly that it is but justifiable to arrange the material and present it in its logical shape. Owing to the fact that Prof. Detlefsen is dealing with the whole piece of chromosome, it is impossible for me to find out the crossover values of Region 1&2 for the respective generations to which the two original males belong. However, we know the value for the whole region, and in order to present the data in the shape it is now,

it is imperative that we assign to Region 1 & 2 a value which we think most nearly true. This value is indicated by a cross in the first line of Table 2. The females used were normal, being considered capable of giving 18.5% of cross-overs within Region 1 & 2. From a cross of this description, we naturally expect an F_1 population giving an intermediate value of crossover between the values of the parents. This opportunity for testing the F_1 generation, however, was not given to the writer but through the kindness of Mr. Clements, the F_1 crossover values for both Experiments were obtained which are shown in the table.

It is readily seen that the F_1 crossover values of both experiments are not high enough to be called intermediate between the parents. Those of the F_2 are still lower. A clearer idea of the F_2 data is better grasped by glancing over the curves in Figure 2. If due allowance were made in the first classes, we can but conclude that a partial dominance of the "low modifiers" must be existing, since the mean total crossover value of the F_1 and F_2 is lower than an arithmetic mean between the original parents.

Now, if we compare the F_2 crossover values of detached piece with those of whole chromosome, we will find that they show up in the same general magnitude, being 5.44% in Experiment 1 and 6.37% in Experiment 2 as compared to 5.817% when the whole chromosome was involved. This direct comparison of F_1 and F_2 data brings out clearly the fact that modifiers of linkage values affect detached portions of chromosome same as they do the whole piece.

Since, as has been mentioned, the low male used in Experiment 2 was from F_{84} generation and the females employed had been subjected to six generations of inbreeding, while those used in Experiment 1 were just normal individuals and the male was from F_{78} , we should expect the standard deviations of the two F_2 populations to show some difference. A glance at that column in the table will

tell that they do differ, and also in such a way as we expected. The standard deviation of Experiment 1 being bigger than that of Experiment 2.

B - Region 4.

As mentioned at the beginning of this paper the purpose of this work is more of the nature to try to throw further light on the whole problem of modifiers of linkage values than merely to secure more data to expand the theme stated in the subject, so I ran a test on Region 4 which is the space between miniature and forked, and it is outside the original region of selection. As it appears in Table 3, this region does not seem to have been influenced by selection. Forty-one females were tested and with an average of 127 offspring per female, the crossover value obtained for the region is 19.75%, which is very close to the recognized value:- 20.4%. Owing to the extremely small number of offspring obtained from some of the females, the distribution table drawn up is rather puzzling. Since selection does not seem to have any effect on this region, the F₂ population should show a normal curve varying around the recognized value. Too much emphasis, however, should not be laid on the distribution we obtained, since quite a number of the females give so few offspring that the degree of reliability of their crossover capacity as reflected in the data is doubtless deceiving. To eliminate this difficulty, females giving less than fifty offspring are left out of consideration, and the resulting distribution is shown in Table 4. A curve plotted from this distribution is shown in Figure 3 with 17% as the modal class.

IV

CONCLUSIONS

From the above discussions of data the following conclusions may be drawn.

TABLE III
Region 4.

Reg. 4	Condition of chromosome females	Number of females	Distribution of crossover values																Total Crossovers	% of Crossovers	offspring per female
			8	10	12	14	16	18	20	22	24	26	28	30	32	34	36				
F1	whole		1		3	4	2	6	4	2	1									18.41	
F2	detached	41	2	3	8	0	1	9	2	2	6	1	2	3	0	1	1	5215	1030	19.75	127

TABLE IV

Generation of chromosome females	Condition of chromosome females	Number of females	Distribution of Crossover values															
			9	11	13	15	17	19	21	23	25	27	29	31	33	35		
F ₂	detached	28	2	0	3	3	6	4	2	0	3	2	1	1	0	1		

This Table is derived from Table III from which females giving less than fifty offspring are left out.

Figure 3.



Plotted from Table IV.

1 Segments of chromosome when separated from the whole piece of chromosome under selection still show low crossover value - a fact showing that modifiers of linkage values affect detached portions of chromosome in the same fashion as they do the whole piece.

2 In a hybridization experiment performed on "low" and "normal" flies with only a segment of the whole piece of chromosome under selection, the mean value of the F_2 generation did not come out quite as high as would be expected on the basis of incomplete dominance. The great portion of the population was grouped in the lower one third of the curve. This phenomenon suggest the existence of partial dominance of the "low modifiers."

3 Selection exercised on regions 1,2 and 3 in the sex chromosome does not affect the crossover value of the region outside of this, as far as we can see from our data.

V

ACKNOWLEDGEMENT.

The writer is very grateful to Prof. J. A. Detlefsen for the opportunity to work on this problem. It is with a deep sense of appreciation to say that but for his helpful suggestions and his generosity in equipping the writer with necessary laboratory conveniences this work would not have been possible.

VI

LITERATURE CITED.

- Bridges, C. B. 1915 A linkage variation in *Drosophila*. Jour. Expt. Zool., vol. 19, pp. 1-21
- Detlefsen, J. A. and Roberts E. 1921 Studies on Crossing Over. Jour. Exp. Zool. vol. 32, no. 2, pp. 333-354.
- Detlefsen, J. A. 1920 Is crossing over a function of distance? Proc. Nat'l. Acad. of Sci. vol. 6, No. 11, pp. 663-670.
- Plough, H. H. 1917 The effect of temperature on crossing over in *Drosophila*. Jour. Expt. Zool., vol. 24, pp. 147-210.
- Sturtevant, A. H. 1919 Inherited linkage variations in the second chromosome. Pub. Carnegie Inst. Wash. D. C., no. 278, pp. 305-341.

VII

Table 5

Region 1 & 2. Experiment 1.

F ₂ ♀	R 1 X	R 2 X	R 1&2 X	Total X	Parental	Total		R 1 X%	R 2 X%	R 1&2 X%	Whole Eg.	
						offsp	offsp				X%	X%
1-2, 1	3	2	0	5	133	138	2.17	1.44	0	0	3.61	
3	1	1	0	2	17	19	5.26	5.26	0	0	10.52	
4	1	3	0	4	37	41	2.43	7.31	0	0	9.74	
6	4	0	0	4	145	149	2.68	0	0	0	2.68	
5	19	10	1	29	205	234	8.11	4.27	.42		12.38	
2	0	0	0	0	26	26	0	0	0	0	0	
4	0	0	0	0	19	19	0	0	0	0	0	
5	5	6	0	11	112	123	4.06	4.87	0	0	8.93	
7-1, 1	0	0	0	0	24	24	0	0	0	0	0	
2	0	0	0	0	13	13	0	0	0	0	0	
3	0	0	0	0	4	4	0	0	0	0	0	
4	9	5	0	14	80	94	9.57	5.31	0	0	14.88	
8	11	13	1	24	336	360	3.05	3.61	.27		6.66	
3	0	0	0	0	3	3	0	0	0	0	0	
4	3	4	0	7	81	88	3.40	4.54	0	0	7.94	
5	5	0	0	5	30	35	14.28	0	0	0	14.28	
12-1, 2	0	0	0	0	16	16	0	0	0	0	0	
3	0	0	0	0	1	1	0	0	0	0	0	
12-2, 1	9	2	0	11	188	199	4.52	1.00	0	0	5.52	
2	2	1	0	3	79	82	2.43	1.21	0	0	3.64	
3	3	1	0	4	135	139	2.15	.71	0	0	2.86	
4	4	4	0	8	194	202	1.98	1.98	0	0	3.96	
8	0	0	0	0	12	12	0	0	0	0	0	
9	13	4	0	17	95	112	11.60	3.57	0	0	15.17	
15	0	0	0	0	1	1	0	0	0	0	0	
1	0	0	0	0	13	13	0	0	0	0	0	
2	5	1	0	6	111	117	4.27	.85	0	0	5.12	
3	1	1	0	2	66	68	1.47	1.47	0	0	2.94	
4	3	2	0	5	96	101	2.97	1.98	0	0	4.95	
5	2	4	0	6	64	70	2.85	5.71	0	0	8.57	

15-1, 5	1	1	2	12	14	7.14	0	14.28
15-2, 2	4	4	8	105	109	3.66	0	7.32
15-2, 3	1	0	1	89	90	1.11	0	1.11
16-1, 4	0	0	0	51	51	0	0	0
16-1, 1	0	1	1	75	75	0	0	1.33
17-1, 1	2	0	2	53	53	3.77	0	3.77
17-2, 2	5	7	12	97	97	5.15	0	12.36
21-1, 1	2	1	3	50	50	4.00	0	6.00
21-1, 2	2	5	7	173	175	1.14	0	4.00
20-2, 4	1	1	2	55	56	1.78	0	3.56
20-2, 1	6	4	10	68	74	5.40	0	13.50
25, 2	1	0	1	66	67	0	0	1.49
25, 6	3	9	12	63	66	13.63	0	18.17
28, 1	2	1	3	90	92	1.08	0	3.25
28, 2	0	1	1	28	28	3.57	0	3.57
Total	133	99	232	3402	3634	2.72	.055	6.37

VII

Table 6

Region 1 & 2. Experiment 2.

F2 ♀♀	R 1 X	R 2 X	R 1&2 X	Total X	Parental Total offsp	R 1 X%	R 2 X%	R 1&2 X% (double)	R 1&2 X%
2-1, 2	0	0	0	0	6	0	0	0	0
3	1	1	0	2	35	2.85	2.85	0	5.7
4	0	0	0	0	52	0	0	0	0
2-2, 1	8	2	0	2	86	8.33	2.08	0	10.41
3	4	2	0	6	172	2.24	1.12	0	3.36
4	4	2	0	6	83	4.49	2.24	0	6.73
4-1, 1	13	7	1	20	206	5.75	3.09	.44	8.84
2	5	1	1	6	107	4.42	.88	.82	5.3
3	3	4	1	7	130	2.18	2.91	.72	5.09
4	1	4	0	5	129	.74	2.98	0	3.72
4-2, 1	4	2	0	6	102	3.7	1.85	0	5.55
2	4	1	1	5	111	3.44	.86	.86	4.3
3	15	3	0	18	136	9.74	1.94	0	11.68
6-2, 2	2	4	0	6	154	1.29	2.59	0	3.88
4	4	3	0	7	185	2.08	1.55	0	3.64
6	1	0	1	1	83	1.19	0	0	1.19
7-2, 1	0	2	0	2	60	0	3.22	0	3.22
5	0	0	0	0	37	0	0	0	0
12-1, 1	4	12	0	16	97	3.53	10.61	0	14.14
2	0	1	0	1	7	0	12.5	0	12.5
4	6	1	0	7	121	4.68	.78	0	5.46
5	10	4	1	14	278	3.42	1.36	.34	4.78
6	6	7	0	13	157	3.53	4.11	0	7.64
12-2, 1	3	1	0	4	147	1.98	.66	0	2.64
3	15	10	2	25	150	8.57	5.71	1.14	14.2
5	1	2	0	3	97	1.0	2	0	3
7	4	1	0	5	95	4	1	0	5
8	6	1	1	7	82	6.74	1.12	1.12	7.86
9	0	1	0	1	25	0	3.84	0	3.84

10	2	5	0	7	76	83	2.4	6.02	0	8.42
14-1, 1	1	4	0	5	31	36	2.77	11.11	0	13.88
2	1	3	0	4	67	71	1.40	4.22	0	5.62
4	0	0	0	0	19	19	0	0	0	0
5	3	0	0	6	95	101	2.96	2.96	0	5.92
6	0	2	0	2	111	113	0	1.76	0	1.76
14-2, 2	0	0	0	0	38	38	0	0	0	0
22-1, 1	2	0	0	2	37	39	5.12	0	0	5.12
2	5	3	0	8	78	86	5.81	3.48	2.32	9.29
3	7	8	0	15	182	197	3.55	4.06	0	7.61
4	5	2	2	7	117	124	4.03	1.61	0	5.64
22-2, 1	12	10	0	22	282	354	3.94	3.28	0	7.22
3	1	0	0	1	22	23	4.24	0	0	4.34
4	1	0	0	1	78	79	1.26	0	0	1.26
25-1, 2	5	2	0	7	141	148	3.37	1.35	0	4.72
25-2, 1	4	5	0	9	118	127	3.14	3.93	0	7.07
2	2	0	0	2	29	31	6.45	0	0	6.45
32-1, 1	1	0	0	1	114	115	.86	0	0	.86
36-1, 1	0	0	0	0	8	8	0	0	0	0
2	2	2	0	4	28	32	6.25	6.25	0	12.5
36-2, 2	0	0	0	0	41	41	0	0	0	0
37-1, 1	2	1	0	3	114	117	1.70	.85	0	2.55
2	0	1	0	1	174	175	0	.57	0	.57
3	0	1	0	3	117	120	1.51	0	0	1.51
4	2	0	0	2	91	93	2.15	0	0	2.15
37-2, 1	1	0	0	1	51	62	1.61	0	0	1.61
2	0	0	0	0	31	31	0	0	0	0
38-2, 1	1	3	0	4	135	139	.71	2.15	0	2.86
Total	187	133	8	320	5547	5867	3.18	2.26	.14	5.44

VII

Table 7

Region 4

F ₂ ♀♀	Parental	Crossover	Total	%
1-1, 1	18	9	27	33.33
4	94	22	116	18.96
5	118	18	136	13.23
6	57	5	62	8.06
8	52	11	63	17.46
1-2, 3	110	18	128	14.06
5	16	4	20	20.00
2	19	3	22	13.63
4	57	21	78	26.92
5	22	9	31	29.03
7	16	5	21	23.89
8	6	1	7	14.28
7-2, 1	373	138	511	27.00
2	179	59	238	24.78
8	48	7	55	12.72
3	131	23	154	14.93
9	132	20	152	13.15
12-1, 1	25	7	32	21.87
3	85	28	113	24.77
4	65	21	86	24.21
12-2, 1	499	117	616	18.99
4	52	11	63	17.46
2	14	2	16	12.56
15-1, 4	276	75	351	21.36
1	42	6	48	12.5
15-2, 1	186	37	223	16.59
2	49	22	71	30.98
16-2, 1	205	54	259	20.84
17-2, 1	263	54	317	17.03

2	83	17	100	17
20-2, 3	105	24	129	19.6
21-1, 2	30	12	42	28.57
4	253	44	302	14.56
21-2, 5	95	22	117	18.8
6	59	7	51	3.56
6	182	29	221	17.44
25	36	20	56	35.71
3	46	19	65	29.23
4	26	8	34	23.52
28	40	5	46	13.04
32	16	5	21	23.80
Total	4185	1030	5215	19.75

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